Flow Velocity Induces a Switch From Active to Passive Suspension Feeding in the Porcelain Crab *Petrolisthes leptocheles* (Heller)

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Abstract. A flow-induced switch in suspension-feeding behavior of the porcelain crab *Petrolisthes leptochcles* was investigated in a laboratory flow tank. Crabs were exposed to two types of experimental water flow to stimulate them to switch from active to passive suspension feeding. In the first experiment, feeding crabs were exposed to a uni-directional accelerating water current, and they switched from active to passive suspension feeding at a mean water velocity of 3.49 cm s^{-1}. In the second experiment, crabs were exposed to flow that was fixed at a constant velocity for at least 10 min, and their feeding behavior in this steady flow was observed. This procedure was repeated, using a range of constant-velocity flows that were successively adjusted to increased velocity levels. Crabs exposed to these different constant-velocity flows fed exclusively actively at flows below 1.5 cm s^{-1} and exclusively passively at those above 4.5 cm s^{-1}. Switches from active to passive feeding occurred throughout the range of constant-velocity flows from 1.5 to 4.5 cm s^{-1}.

Changes in feeding activity rate induced by an increase in water velocity were measured. The mean activity rate of active feeding (1.05 Hz) was 3.4 times higher than that of passive feeding (0.31 Hz).

The porcelain crab's ability to switch feeding modes in response to increased water velocity probably enhances energetic feeding efficiency in two ways. First, the passive feeding activity rate is lower than the active one and should reduce energetic expenditure. Additionally, the flux of suspended food increases with water flow velocity, so passive feeders are likely to catch more food per unit time than active feeders do. The ability to switch feeding modes is quite similar to that already described for balanomorph barnacles and appears to represent convergent evolution of flexible feeding behavior in response to variable water flow environment.

Introduction

Many benthic marine invertebrates can switch their mode of feeding in response to changes in environmental conditions. For example, in the grapsid crab *Gaetice depressus,* Depledge (1989) observed several feeding modes including scavenging, predation, deposit feeding, and suspension feeding, noting that the particular mode observed depended on the availability of different food types. Turner and Miller (1991) showed that a sufficient water movement would induce deposit-feeding chaetopterid polychaetes to extend their tentacles into the current and switch to suspension feeding. Okamura (1987) inferred a switch from ciliary to tentacular suspension feeding that was induced in bryozoans by particle size and flow velocity. According to foraging theory, such behavioral switches tend to enhance feeding efficiency (as measured in some energy currency, such as net energy gained per unit time, or the ratio of energy gained to energy spent) and thus increase fitness (Schoener, 1971; Pyke, 1984).

In aquatic habitats suspension feeding is a widespread mechanism for obtaining energy and materials from the water column, and representative suspension feeders are found in most major animal phyla (Jorgensen, 1966). Suspension feeders can be generally categorized as either active or passive. Active feeders spend their own metabolic energy to pump water past feeding structures, whereas

passive feeders rely on the external source of energy in ambient currents for delivery of food particles to feeding structures (LaBarbera, 1984). Some animals, such as barnacles and tunicates, can suspension feed both actively and passively (LaBarbera, 1977).

The passive feeding mode in porcelain crabs has received only brief mention in the literature (*e.g.,* Wicksten, 1973; Kropp, 1981), probably because the velocities of incidental flow induced by aeration devices are typically too low to produce active feeding in laboratory aquaria.

Here, we quantitatively describe a flow-induced switch from active to passive suspension feeding in the porcelain crab *Petrolisthes leptocheles*. A behavior indexing technique was employed to provide both qualitative information on feeding behavior components and quantitative data on feeding activity rates. These data were amenable to standard time-series analysis (fast Fourier transforms) for quantitative differentiation of active and passive feeding behaviors on the basis of differences in their activity rates (frequencies). Our results supplement the list of species that are known to switch from active to passive suspension feeding when water currents are sufficiently high.

Materials and Methods

P. leptocheles was collected in the Gulf of Eilat, Red Sea, Israel, from under stones in the shallow subtidal (to 0.5 m depth) off the H. Steinitz Marine Biology Laboratory, the Interuniversity of Eilat, Israel. Specimens were kept in unfiltered, flowing seawater. Experiments were carried out at the Laboratory from January through February 1992 and in February 1993. Throughout all experiments, the water temperature was 25–26°C.

To control water flow precisely, a flow-pattern generator was used. It consisted of a recirculating flow tank (Vogel and LaBarbera, 1978) modified by the addition of computer-controlled water flow. Water movement was produced by computer programs that were interfaced, through a digital-to-analog circuit, with a motor-driven propeller immersed in the flow tank (Fig. 1a). To record behavior and water flow simultaneously, laser optics (Strickler, 1985), fiber optic lamps, close-up lenses, and video equipment were used (Fig. 1b). This video-optical system allowed close-up observation (image magnification from 10 to 30×) of animal motions, as well as visualization of water flow as indicated by the movements of brightly illuminated particles naturally suspended in unfiltered seawater. For videorecording during experiments, all animals were placed on a gravel-filled petri dish which was then positioned on the floor of the flow tank so that the anteroposterior axis of the crab was perpendicular to the axis of flow direction while its mouth faced towards the camera.

Two computer programs were used to produce two types of experimental water flow change. In the first experiment, water was continually accelerated linearly past a suspension feeding crab at a rate of 0.15 cm s^{-2}, with a program that produced the repeating pattern of alternating accelerating and decelerating flows shown in Figure 2. The suspension-feeding behavior of one crab at a time was videorecorded during one acceleration period. During the following deceleration period, the crab was removed from the flow tank, and the flow tank motor was shut off. Another crab was placed in the tank, and when feeding began, the motor was turned on to expose the crab to the same accelerating flow stimulus that the previously tested crab experienced. This protocol was repeated until 19 crabs had been tested. The computer program assured that the water flow acceleration stimulus was the same for each crab.

In the second experiment, a different computer program was used to maintain a constant water flow velocity (acceleration = 0) for an extended period. Here, a crab was placed in the flow tank, first in nearly still water (less than 2 mm s^{-1}, flow tank motor off), and when feeding began, its behavior was videorecorded for 10 min. Then the crab was removed, the motor was turned on with the computer program at a fixed setting, and flow in the tank was allowed to stabilize (for 1 min) at a steady flow velocity of 0.5 cm s^{-1}. The crab was then put back into the tank, and when feeding began, its behavior was videorecorded for another 10 min with flow constantly maintained at 0.5 cm s^{-1} (*i.e.,* no change in velocity) throughout the recording period. This procedure was repeated with the same crab, at successively increased, constant velocity flows (1.0, 1.5, 2.5, 3.5, 4.5, 5.5, and 6.5 cm s^{-1}). Each velocity was maintained for 10 min while feeding behavior was videorecorded. The entire protocol was repeated until 11 crabs had been tested.

Flow velocities local to the animal (from 2 to 6 mm above the distal edges of extended feeding fans) were measured by frame-by-frame tracking of the movements of back-lit particles suspended in flowing water as described by Trager *et al.* (1990).

Time-series data on feeding-motion cycles were obtained by playing back the videorecordings. Components of cyclical feeding behavior were identified, and a numerical value was assigned to each one, producing a behavioral index. For example, crab feeding-fan movements during active suspension feeding consist of three easily identified components (transfer of food particles from the fan to the mouth, upward extension of the fan, and a forward and downward capture stroke) that occur over and over again in the same sequence. These three components were assigned index values 1, 2, and 3, respectively. Behavioral time-series data were taken every 0.04 s (every video frame), over a total period of 81.9 s (more than 50 behavior cycles), by assigning the appropriate index value to the behavioral component observed
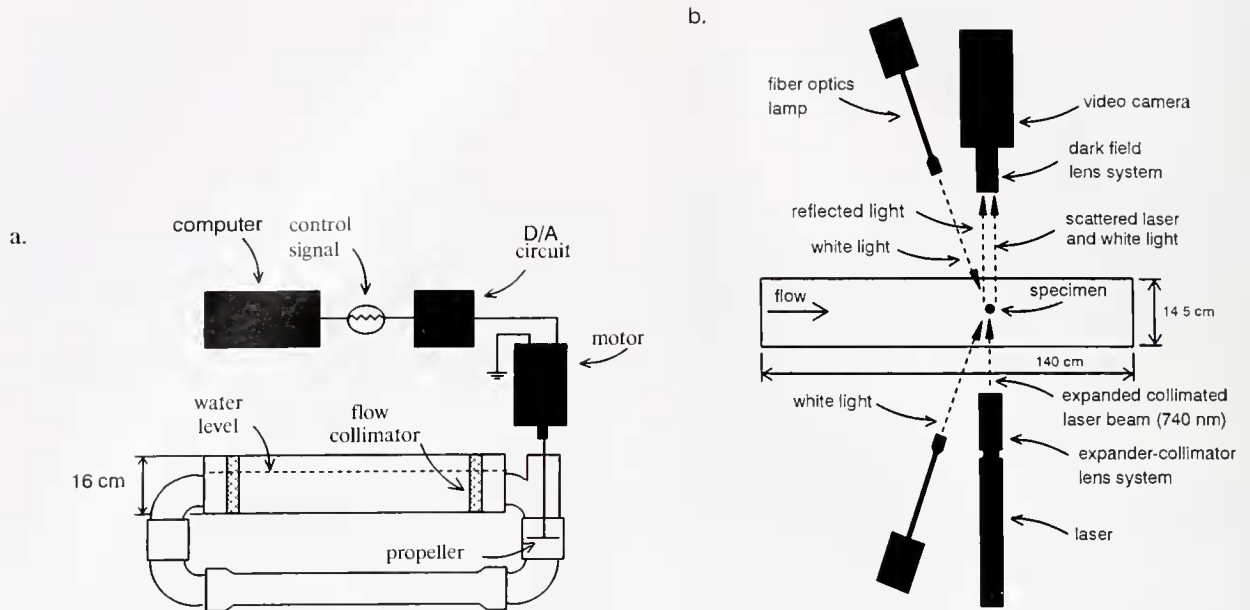
b.

a.

Figure 1.   Apparatus for controlling water flow. (a) Side view of computer-controlled flume. Computer programs generate digital signals and send them to the digital-to-analog (D/A) circuit, where they are converted to analog signals to the 12 V DC flume motor. This system allows precise repetition of experimental flow regimes. (b) Top view of flow tank showing positioning of video camera, lens system, light sources, optical paths, and specimen. Backlighting was provided, either by a laser in line with the specimen and the video camera or by a fiber optics lamp at an angle of about 25° to a line through the specimen and video camera. The dark-field lens system was used only with the laser. The two backlighting sources were not used simultaneously. Both techniques provide a similar dark-field image in which naturally suspended particles in flowing seawater appear as bright points of light against a dark background, for flow visualization. Frontlighting by fiber optics was also provided for bright-field illumination of moving feeding appendages.

in each consecutive video frame. Plotting the indexed behavioral data against time produces a wave form, or cyclical curve, that illustrates the changes in feeding com-
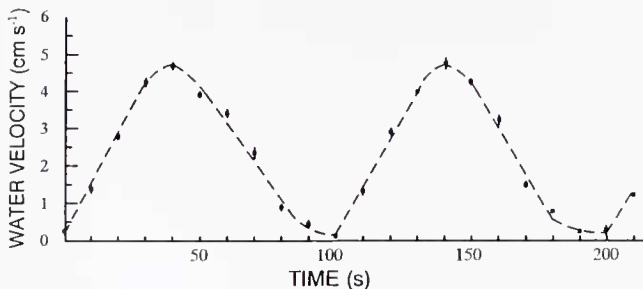

Figure 2.   Repeating pattern of alternating accelerating and decelerating flows producing replicable, linear, water flow acceleration inducing porcelain crabs to switch from active to passive feeding. Feeding behavior was monitored only while flow accelerated. Flow deceleration simply reset the water velocity back to its original starting level, so that the next animal tested could be exposed to the same flow acceleration stimulus that the previously tested crab experienced. This flow pattern was generated by a triangle-wave signal from a computer program. Each point is the mean velocity of 20 suspended particles tracked from 0.5 s before to 0.5 seconds after the time indicated on the abscissa. Vertical bars show standard errors.

ponents and activity rhythms that concur with changes in flow velocity. The cyclically fluctuating numerical data produced by behavioral indexing are also suitable for analysis with fast Fourier transforms in the frequency domain, so that the distinct activity rates (frequencies of cyclical feeding-fan motions) distinguishing active versus passive feeding could be identified.

Results

Although active and passive feeding were easy to distinguish on the basis of activity rate and orientation of feeding structures, there was a period of transition during the acceleration experiments when, as water was gradually accelerating, the crabs exhibited intermediate feeding behaviors with characteristics of both modes. These flow-induced behavioral changes, from active to intermediate to passive suspension feeding, are described below.

In very calm water (<1 cm s^{-1}), the crabs always suspension feed actively, by simultaneously extending both of their setose third maxillipeds to form two extensive spoon-shaped feeding fans (Fig. 3a). Both fully extended fans are then flexed, sweeping rapidly forward, downward, and laterally toward the mouth through a volume of water
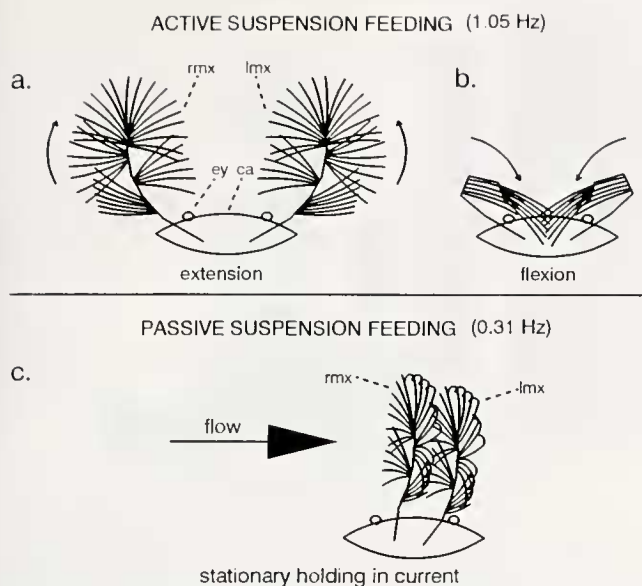
ACTIVE SUSPENSION FEEDING (1.05 Hz)

PASSIVE SUSPENSION FEEDING (0.31 Hz)

Figure 3. Diagram of porcelain crab (front view) carrying out active suspension feeding, which occurs only in slow ambient flow (on average, at flow velocities less than about 3.5 cm s^{-1}), and passive suspension feeding, which occurs only in fast flow (on average, at flow velocities greater than about 3.5 cm s^{-1}). (a) During active feeding, the third maxillipeds are spread laterally and then unflexed so that the setae spread out to form a spoon-shaped fan. Abbreviations: ca, carapace; ey, eye; lmx, left third maxilliped; rmx, right third maxilliped. (b) The next component of active feeding consists of the fan being flexed and sweeping forward, downward, and laterally towards the mouth for removal and transfer of trapped food particles to the mouth. (c) During passive feeding, both feeding fans are held stationary with the concave sides facing into the current. Arrow indicates water flow direction.

(Fig. 3b). Next, the fans contact the second maxillipeds, which remove trapped food particles that are passed to the mouth. This entire sequence is performed repeatedly for as long as active feeding lasts. This feeding behavior is similar to that described by Nicole (1932) for the porcelain crab *Porcellana longicornis*, except that *P. longicornis* usually sweeps its left and right fans alternately, whereas in this study, *P. leptocheles* always swept both fans simultaneously.

When the accelerating water reaches a velocity of about 1.5 to 2 cm s^{-1}, intermediate behaviors begin with characteristics of both active and passive feeding. The crabs still sweep both fans rapidly and rhythmically, but begin to angle the concave side of the left fan towards the current so that the capture stroke begins in the upstream direction. This is not possible for the right fan because the structure of the third maxillipeds does not permit a sweep (flexion) laterally away from the animal (see Fig. 3). Thus, the right fan, unlike the left fan, continued to repeatedly extend and flex, as in calmer water.

As the water continues to accelerate, the frequency of the cyclical motions for both fans decreases because a new behavioral component appears. Immediately after fan extension, there is a pause, during which the fan is held fully extended and stationary, with the concave side facing upstream, positioned for passive suspension feeding in the current (Fig. 3c). The duration of this stationary fan-holding behavior steadily increases, up to a point, as the water velocity continues to increase, and the sweep into the current of the left fan is quickly phased out, so that stationary holding is followed by a twisting, forward, downward, and proximolateral flexion similar to that of active feeding. Extension of the fans into the current, holding in a stationary concave-upstream position for a time, and then flexion for particle removal is the typical cycle of passive feeding behavior.

In a few cases, the water was accidentally accelerated very rapidly (*e.g.*, around 10 cm s^{-2}) when the flow system was turned on with the motor already at a high-speed setting. In these cases, the crabs switched from active to passive feeding almost instantaneously, with no evident intermediate behavior. But in the controlled experimental flow that was gradually accelerated (at a rate of 0.15 cm s^{-2}), there was always a period of intermediate behavior. Thus, switch velocity, which is defined here as the ambient water velocity in accelerating flow at which a suspension-feeding animal switches from active to passive feeding, was determined as the point at which the stationary holding component of passive feeding (which is the primary distinguishing characteristic of the passive feeding mode) is longer than 1 s.

The flow-induced behavioral changes from active to intermediate to passive suspension feeding are depicted graphically in an indexed-behavior time-series plot (Fig. 4) that displays both qualitative and quantitative (frequency) information.

The mean switch velocity for all crabs tested in accelerating flow was 3.49 cm s^{-1} (Fig. 5). The mean cycle frequencies of active (1.03 Hz) and passive (0.31 Hz) feeding motions are compared in Table 1. The passive feeding rate was much more variable than the active feeding rate, and the mean activity rate of actively feeding crabs was 3.4 times greater than that of passively feeding crabs.

In the constant-velocity experiments, all 11 crabs tested fed exclusively in the active mode at velocities less than 1.5 cm s^{-1} and exclusively in the passive mode at velocities greater than 3.5 cm s^{-1}. Switches from active to passive feeding occurred from 1.5 to 3.5 cm s^{-1} (Fig. 6). In Figure 6, a crab was considered to have switched to passive feeding if it was observed to perform any passive feeding at all during a 10-min period. Five crabs switched in the middle of an observation period, and two of these switched back and forth several times during that period. For these five crabs that performed both active and passive feeding during an observation period, the mean percent of time
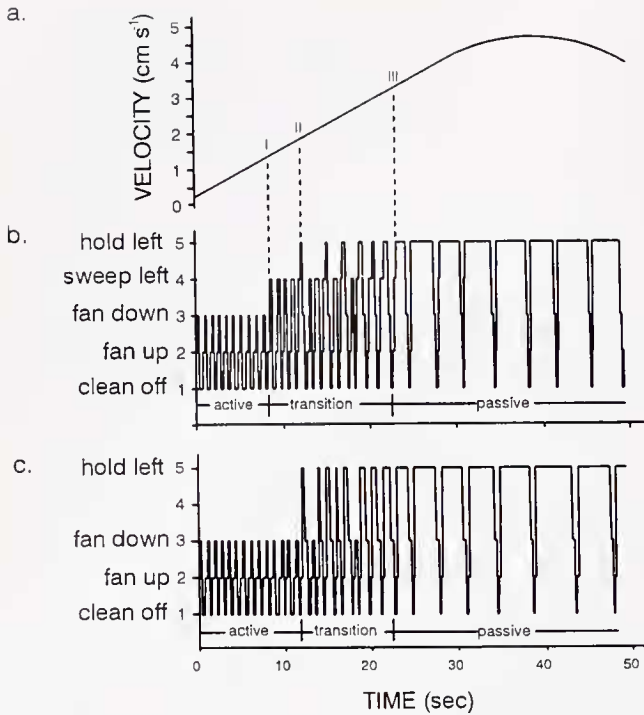
Figure 4.   Behavioral change from active to intermediate to passive suspension feeding induced by linearly accelerated unidirectional water flow. (a) Linear change in flow velocity inducing the behavioral changes depicted graphically in (b) and (c), which show numerically indexed components of cyclical feeding behavior plotted against time. Each behavioral component and its assigned index value is listed on the ordinate, and the occurrence of any component is indicated by a peak or plateau in the curve at the appropriate level. The length of each horizontal portion of the indexed behavior curve indicates the duration (seconds) of a behavioral component. Steeply inclined rises or drops of the curve show when, from one video frame to the next, a behavioral component has changed. Thus, changes in activity rate (frequency) are indicated by changes in the horizontal distance between curve peaks, and changes in behavioral components are seen as changes in the height of the curve peaks. (b) Indexed behavior time series for the left feeding fan. Active feeding is rapid (0.95 Hz), occurs in slowly moving water, and consists of only 3 components (clean off, fan up, and fan down). The beginning of intermediate behavior, with characteristics of both active and passive feeding, first appears at a velocity of about 1.5 cm s^{-1}, when the behavior curve suddenly jumps up to an index value of 4 (sweep left). The time and velocity at which this new component appears is indicated by (I) on the velocity curve. The activity rate also slows down somewhat during this transition period, with the appearance of the "hold left" component [stationary holding of the fan into the current (index value 5); its first appearance is indicated by II on the velocity curve]. Strict passive feeding begins at a velocity of about 3.2 cm s^{-1} (see III), when the length of the hold left component is greater than 1 s. (c) The right fan shows changes in activity rate that are very similar to those of the left fan, but there is no sweep left (index value 4) component. The activity rate of the right fan during passive feeding is also considerably lower than that of strictly active feeding.

spent in passive feeding was 40.2% (SD = 13.2). The remaining six crabs fed only actively during the entire 10-min observation periods at low velocities, and then
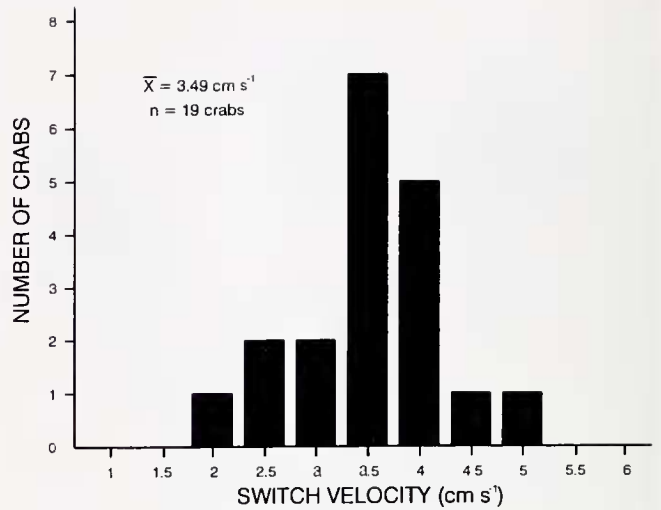

Figure 5.   Switch velocities (*i.e.,* the ambient water velocities at which crabs switched from active to passive feeding) in unidirectional accelerated flow. Frequency histogram of the number of porcelain crabs in different switch-velocity classes. Each class is the median water velocity indicated on the x axis $\pm$ 0.25 cm s^{-1}. Water velocities at the behavioral switch point were measured by calculating the mean velocity of 20 suspended particles video-tracked from 0.5 s before, to 0.5 s after the switch. A switch-velocity value for an individual crab is the average of the left and right fan values.

switched to feeding entirely in the passive mode throughout the observation periods at higher velocities.

Because the flow-induced changes exhibited by all crabs were similar, only two characteristic time series (2048 data points for each feeding fan of one animal) were chosen from the flow acceleration experiments for spectral analysis. Fast Fourier transforms of indexed behavior time series (portions of which are plotted in Fig. 4b and c) show that active and passive feeding behavior can be distinguished by their respective frequencies (Fig. 7). The power spectrum curve in Figure 7, produced by plotting the results of the fast Fourier transforms, indicates the relative importance of different component frequencies

Table I

Activity rates measured for active and passive suspension feeding in 19 porcelain crabs

Feeding mode	Mean cycle frequency* (Hz)	Variability (%)	
		Within individuals	Between individuals
Active	1.05	6.4	12.5
Passive	0.31	27.0	19.4

* Calculated by measuring length (in seconds) of 10 consecutive cycles of active and passive feeding that were recorded on videotape.
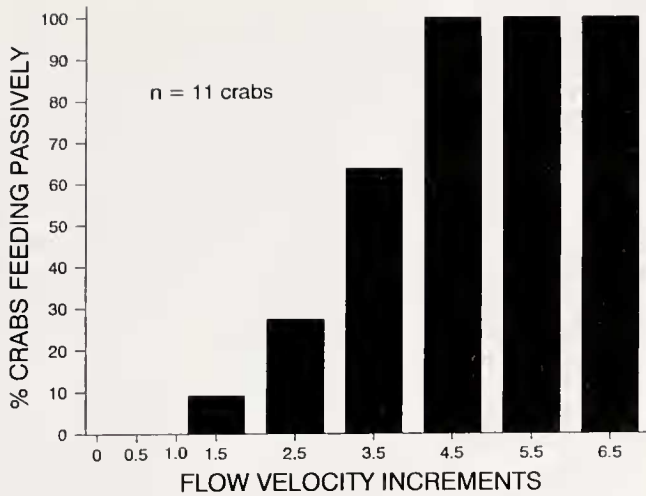
Figure 6. Percentage of crabs feeding passively over a range of constant velocity flows. Each constant flow velocity indicated on the x axis was maintained for 10 min. All crabs fed only actively from 0 to 1.0 cm s^{-1}. An increasing percentage of crabs switched from active to passive feeding over the range of 1.5 to 4.5 cm s^{-1}. At flows of 4.5 cm s^{-1} and above, all crabs fed exclusively in the passive mode.

Particle capture rates are also predicted to be higher during passive feeding than during active feeding because passive feeding occurs only in relatively high-velocity flow, when fluid flux—and thus food flux to capture structures—should be greater than in calm water in which active feeding occurs.

Passive feeding is likely to be more efficient than active feeding for another reason. The proportion of total feeding time during which a fan is collecting particles is much greater for a passive feeder than an active feeder. The proportion of total feeding activity time that a fan was

of feeding-fan movements. Thus, a distinct peak on the power spectrum curve indicates a dominant activity rate, or frequency (on the x axis directly below the peak), that characterizes a distinct feeding mode. For both the left and right fans, two dominant power spectrum peaks represent the distinct activity rates of active and passive feeding. Several peaks between the active and passive peaks represent intermediate frequency behaviors that occurred during the transition from active to passive feeding.

Discussion

Not all suspension feeders are able to switch between active and passive modes. The switch may increase feeding efficiency in at least several ways. First, passively feeding crabs are able to depend on an external ambient current to deliver suspended food particles to feeding structures; they therefore do not spend their own metabolic energy to pump water past food-capturing structures. They are also able to orient their feeding appendages optimally with respect to current direction. Baumiller (1988) demonstrated that fluid flux through a concave model filter (a concave-shaped mesh) oriented perpendicular to the flow with the concave side facing upstream was greater than fluid flux through a similarly positioned planar mesh. Spielman and Goren (1968) showed that particle capture efficiency depends on the orientation of filter fibers. These facts together offer an explanation for the consistent passive-feeding orientation of crab feeding fans perpendicular to flow direction, with the concave side facing upstream (see Fig. 3c).
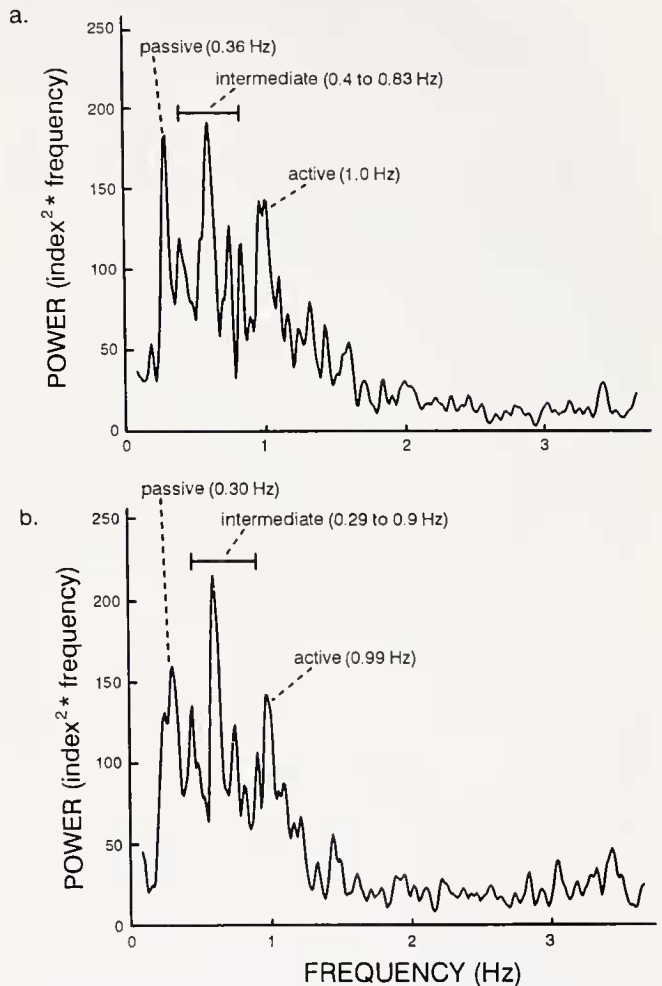

Figure 7. Active and passive suspension feeding are distinguished by their respective activity rates, or frequencies: (a) right fan; (b) left fan. Plotting the results of fast Fourier transforms (Press et al., 1986) of indexed time-series data on feeding motion cycles (portions of which are plotted in Figure 4b and 4c) yields two power spectra that indicate the relative importance of the different frequency components of active, intermediate, and passive feeding behavior. In both the right and left fan plots, two distinct power spectrum peaks represent the distinct frequencies that characterize active and passive feeding. Several peaks between the active and passive peaks represent intermediate-frequency transition behaviors with characteristics of both active and passive feeding.

held stationary into the current during passive feeding was 87% (the other 13% of time was occupied by fan flexion, clean off, and extension). During active feeding, however, the fan is trapping particles primarily when a spread-open fan is swept through the water, and this sweep occupied only about 20% of feeding activity time (the other 80% was occupied by folding setae, cleaning them off, and extending the fan for the next sweep). Thus, the ratio of food catching time to food handling time (a reflection of energetic feeding efficiency) is greater for a passive feeder than an active feeder.

Active feeding should be more efficient than passive feeding only when ambient flow is so low that the bulk of the water, and thus the suspended food particles, will move around rather than through a stationary extended fan. This effect has been demonstrated for the barnacle *Semibalanus balanoides* by Trager *et al.* (1990), who showed that a dye stream aimed slightly (2 mm) above the geometrical center of an extended barnacle feeding fan flowed between the filter elements near the fan's center at an ambient flow speed greater than 3.5 cm s^{-1}, but was diverted completely around the entire fan at a lower ambient flow speed of 0.5 cm s^{-1}. This effect is also predicted by the "leakiness" model of Cheer and Koehl (1987) which describes, as a function of flow speed, bristle spacing, and bristle diameter, how much fluid leaks between the elements of bristled appendages of small organisms, as opposed to how much goes around the entire appendage. When passive feeding becomes less efficient than active feeding (at some ambient flow velocity that can be predicted to be less than, but near, the crab's mean switch velocity of 3.49 cm s^{-1}), a crab must create the relative flow velocity past the filter needed to increase leakiness by actively sweeping its fan rapidly through the water. Therefore, it is the effect of flow velocity on fluid flux (and thus suspended food flux) to the filter that appears to determine the ambient flow velocity at which an animal switches from active to passive feeding.

The factors responsible for the large difference in activity rate between active and passive suspension feeding of porcelain crabs remain obscure. For effective active feeding, the animal must sweep its fans rapidly to pump new water within reach of feeding structures. Thus, a fan not only needs some degree of leakiness for particle capture, but also must have some "non-leakiness" so it can act as a paddle that pushes water past the animal. There are physical and energetic limits on how fast the animal can pump water. Even if these limits are not reached, pumping too fast may result in inefficient processing of the water moving past the animal. This inefficiency might be due not only to the increase in energy cost at a high pumping rate but also to the reduction in particle retention as drag forces increase and allow particles that contact the filter to be carried away by the current. The active

feeding activity rate may represent a trade-off between maximizing flow rate (and thus food flux to the vicinity of the filter) and maximizing food particle capture rate.

The passive feeding activity rate is determined primarily by the length of time a feeding fan is held stationary into the current. In the passive mode, a feeding fan can capture particles without rapid sweeping if it is simply held in position (concave-upstream) for extended periods. Thus, muscular activity rate (and presumably metabolic energy expenditure) is considerably reduced by switching from active to passive feeding when ambient water currents are strong enough.

For the porcelain crab *P. leptocheles* and the barnacle *S. balanoides,* both of which inhabit wave-swept environments, flow velocities are commonly well above the switch velocities of around 3 to 3.5 cm s^{-1} measured in the laboratory. In this study, field measurements taken every 0.5 s over 24 hours with an S4 Interocean current meter, in shallow water (0.5 m) in the crabs' habitat in the Gulf of Eilat, gave a mean flow speed of 15.5 cm s^{-1} (SD = 8.2, maximum = 50.5 cm s^{-1}). Moreover, when first taken into captivity, both species began to feed passively if currents were slightly more than 3 cm s^{-1}, but did not feed at all for 1 or 2 days if kept in calm water (<1 cm s^{-1}), then began to feed actively. This suggests that the animals are accustomed to feeding mainly in the passive mode, and a period of starvation is required to induce feeding in the presumably more energy-demanding active mode. In nature, passive feeding may be the dominant mode for these animals because currents are usually sufficiently high. Active feeding in the natural habitat probably occurs only in restricted flow situations, such as tide pools at low tide or very quiet bays and estuaries when tidal currents are weak or absent. In the laboratory, active feeding has appeared to be the dominant mode only because flow velocities in typical observation aquaria are usually lower than the behavioral active-to-passive switch threshold.

Porcelain crabs and balanomorph barnacles demonstrate striking similarities in suspension-feeding structures and behavior. Although the animals are from different major crustacean taxa (Malacostraca and Cirripedia, respectively; Bowman and Abele, 1982), both possess moveable, scoop-shaped, setal feeding nets that can be oriented concave-upstream to current direction. Both are capable of tracking oscillating flow with high precision (Trager *et al.,* 1992), and both can switch from active to passive feeding in the presence of sufficiently rapid water currents. This suggests that other benthic crustacean species with jointed moveable suspension-feeding apparatus (*e.g.,* Hippid sand crabs and suspension-feeding hermit crabs) may also exhibit comparable convergent structural and behavioral adaptations for suspension feeding in variable flow regimes.

Acknowledgments

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